

## Contribution to the Gametophyte Morphology of the Fern Genus *Lomagramma* J. Sm. in India\*

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ABSTRACT.—The gametophyte development of *Lomagramma sorbifolia* (Willd.) Ching has been studied. Spore germination is of the polar and *Vittaria*-type. Prothallial development is either of the *Adiantum*-type, or more rarely of the *Drynaria*-type. This *Adiantum*-type is unusual among most of the other genera of the lomariopsidoid ferns. The *Drynaria*-type of gametophyte development is more characteristic of the lomariopsidoid ferns. Older prothalli are cordate and naked throughout. Early development seems to be somewhat plastic and perhaps of limited usefulness as a character for systematic purposes.

*Lomagramma* J. Smith is a genus of about 15 species ranging from northeastern India to Tahiti and into tropical America. It is represented by a lone species, *Lomagramma sorbifolia* (Willd.) Ching, in India, where it is known to occur in Garo Hills and Lakhimpur in the state of Assam (Chandra, 2000). The plants are scandent, large, terrestrial, and shade-loving growing mostly near streams in dense tropical forests. The species is very similar to *Lomariopsis* Fée and *Stenochlaena* J. Sm. in habit but has distinctive bathyphylls and anastomosing veins.

Christensen (1938) considered the genus *Lomagramma* as acrostichoid, probably of dryopteroid origin. Holttum (1947, 1949, 1954) for the first time grouped the Lomariopsidoid genera in a separate sub-family Lomariopsidoideae under the family Dennstaedtiaceae. Alston (1956) raised the status of the sub-family to the family level (Lomariopsidaceae), which was later followed by Nayar (1974) and Pichi-sermolli (1877). Ching (1978) segregated *Lomagramma* and *Lomariopsis* as an independent group constituting a separate family Lomariopsidaceae (excluding other Lomariopsidoid ferns), possibly derived from Bolbitidaceae.

Bower (1923–28) and Holttum (1949) pointed out that the comparative morphology of fern gametophytes could be of significance in understanding evolutionary relationships. According to Stokey (1951, 1960, 1964), Atkinson and Stokey (1964), and Atkinson (1973) comparison of gametophyte structure and their development strengthens our understanding of the relationships among various genera and higher groups. They further indicated that useful data might be found in spore germination pattern, the manner of cell plate

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development, meristematic region development, and in the type of early prothallial development.

Morphologically, the family Lomariopsidaceae is poorly known except for details regarding the sporophyte of *Bolbitis* and *Egenolfia* (Nayar, 1950, 1951, 1955, 1956, 1960, Nayar and Kaur, 1964), *Elaphoglossum* (Bell, 1950, 1951a, 1951b, 1955, 1956) and the rhizome morphology of *Lomagramma sorbifolia* (Chandra, 1989).

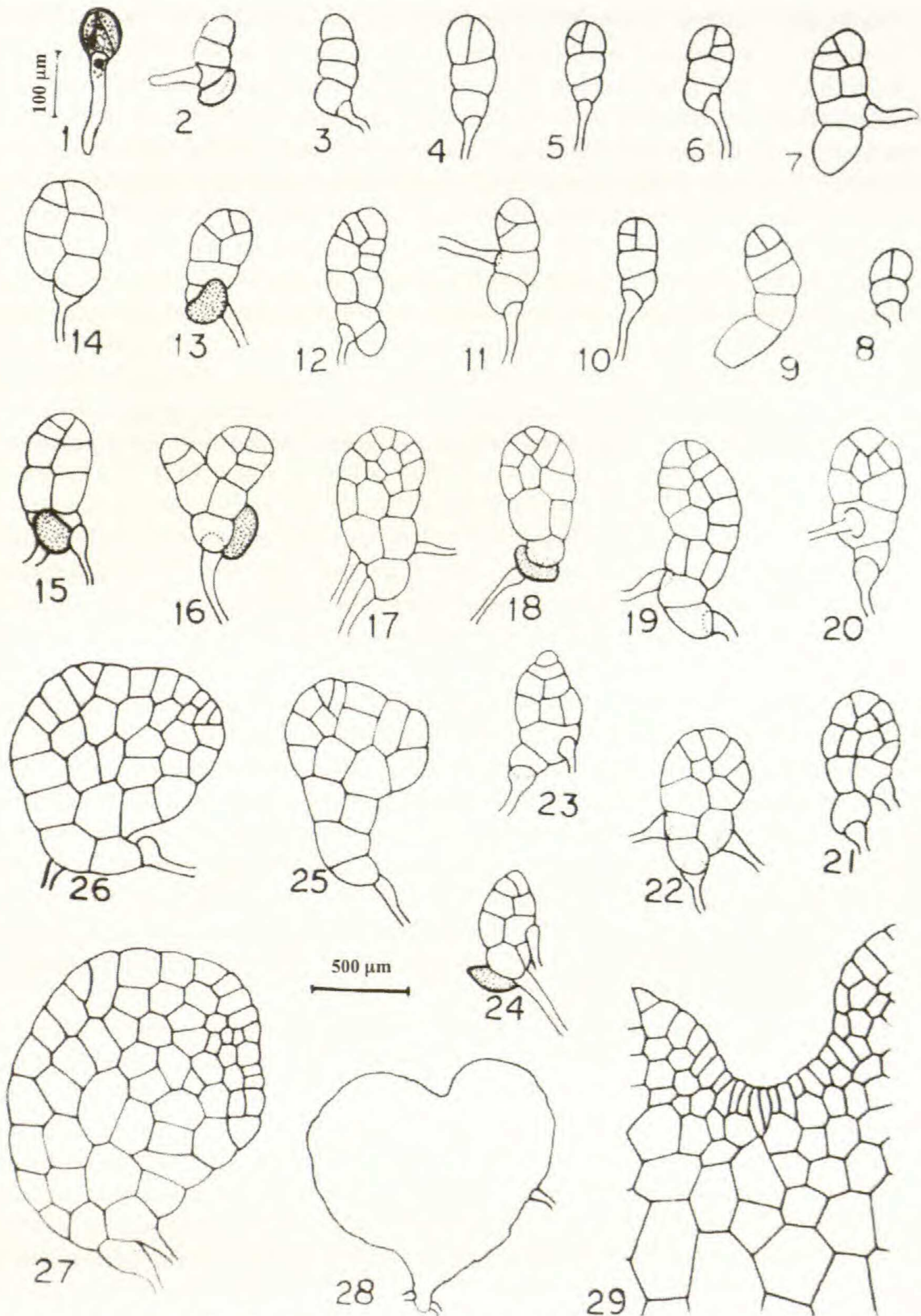
Prothallial morphology in the family Lomariopsidaceae is known only for *Bolbitis* (Nayar, 1960), *Egenolfia* (Nayar and Kaur, 1964, 1965), and *Elaphoglossum* and *Rhipidopteris* (Stokey and Atkinson, 1957). Few details are known about the gametophyte of *Lomagramma sinuata* (Atkinson, 1973). The present study aims at describing the pathway of prothallus development in *L. sorbifolia* and comparing that development with that seen in related ferns.

#### MATERIAL AND METHODS

The present study is based on material collected from Assam (*S. Chandra, LWG 12594*). Fresh spores were surface sterilized with sodium hypochlorite (2%) and thoroughly washed with sterilized water. The sterilized spores were sown onto Petri dishes containing Parker and Thompson's nutrient media (Klekowski, 1969) jelled with 1% agar at 5.4 pH. The cultures were maintained at  $22 \pm 2^\circ\text{C}$  under 600 ft. C. of light from four fluorescent lamps placed horizontally above the culture dishes. All observations on morphology and development of the gametophytes are based on these laboratory cultures. To study cellular structure, the gametophytes were mounted in a 2% acetocarmine solution, which induced partial plasmolysis of the cells rendering the cell outlines clear. Drawings were made using a camera lucida.

#### RESULTS

Spores are monolete, planoconvex to somewhat concavoconvex in lateral view, having a granulose exine, devoid of perine (Nayar and Kaur, 1965) and  $19 \times 27 \mu\text{m}$  in size (average of 10 readings in each plane of spores selected at random), swelling to  $24.5 \times 34 \mu\text{m}$  after acetolysis. They germinate within 15–20 days of sowing. At germination an unequal division by a wall perpendicular to the polar axis (parallel to the equatorial plane) of the spore delimits a large, densely chlorophyllous, hemispherical prothallial cell from a small, lens-shaped, and very sparsely chlorophyllous rhizoid initial cell next to the proximal pole of the spore (Fig. 1). The rhizoid initial protrudes through the laesural aperture and elongates parallel to the polar axis of the spore as a slender, highly vacuolated rhizoid. Meanwhile, the prothallial cell enlarges, elongating along the equatorial plane of the spore, splitting open the spore-coat at the laesural region and dividing by a wall parallel to the polar axis (perpendicular to the first wall) of the spore in such a way that the rhizoid is attached laterally to the basal one of the two daughter cells (Figs. 2, 3); this basal cell does not take any further part in prothallial development. Its sister



FIGS. 1-29. Stages in the development of the gametophyte of *Lomagramma sorbifolia*. 1. Spore germination. 2-3. Uniseriate germ filament. 4. Initiation of plate formation by oblique division of the terminal cell. 8-9. Initiation of plate formation by vertical division of the terminal cell. 5-7 and 10-13. Germ filament showing early formation of apical cell. 14-15. Germ filament showing the formation of a broad prothallial filament. 16. Branched germ filament. 17-25. Germ filament showing establishment of apical cell. 26-27. Young gametophyte showing multicellular meristem. 28-29. Cordate gametophyte.

cell elongates further along the equatorial plane and divides repeatedly by walls parallel to its basal wall (parallel to the polar axis of the spore) forming a short germ filament composed of short, barrel-shaped, and densely chlorophyllous cells (Fig. 3). Spore germination, thus, is of the typical *Vittaria*-type as described by Nayar and Kaur (1968, 1971), the first rhizoid elongating along the polar plane of the germinating spore and the germ filament elongating along the equatorial plane and perpendicular to the first rhizoid. However, due to the physical obstruction provided by the spore coat, the emerging germ filament is often slightly deflected from the equatorial plane.

When the germ filament is three to five cells long, formation of a prothallial plate is initiated by an abrupt change in the plane of wall formation in the terminal cell and often extending to the penultimate cell. Instead of dividing by walls perpendicular to the long axis of the germ filament, these cells divide by walls parallel to the long axis so that the germ filament at its anterior end becomes two tiered. Commonly the wall formed in the terminal cell is oblique (Fig. 4) so that one of the daughter cells is larger with a broader anterior end. Another wall oblique to this wall formed in the larger daughter cell delimits a wedge-shaped apical meristematic cell (Figs. 5–7, 13). In some cases the first division of the terminal cell is parallel (instead of oblique) to the long axis of filament (Figs. 8, 9) followed by an oblique division in this cell to delimit a wedge-shaped apical meristematic cell. Thus, a transverse row of three daughter cells is formed, of which the middle one is wedge-shaped and acts as a meristematic cell (Fig. 10). This type of prothallial development is termed the *Adiantum*-type (Nayar and Kaur, 1969, 1971). The meristematic cell cuts off a series of narrow daughter cells alternately against its oblique sides and these daughter cells, by successive anticlinal and periclinal divisions, form an expanded, one-cell-thick, obovate prothallial plate (Figs. 18–20). Daughter cells of the meristematic cell grow and divide rapidly so that the anterior region of the prothallus on either side of the meristematic cell progressively extend anterior to the level of the meristematic cell, ultimately making the young prothallus cordate (Figs. 28, 29).

A second abrupt change in the plane of cell divisions occurs in the apical meristematic cell when the young prothallus is distinctly cordate. Instead of dividing by walls parallel to its oblique sides, the apical cell divides by a transverse wall, cutting off its wedge-shaped basal region from the larger anterior region, which then divides repeatedly by longitudinal walls to form a plate of 3 or 4 narrow cells. These cells constitute a pleuricellular meristem (Figs. 26, 27) in which all cell divisions are longitudinal. Ultimately a central midrib is established behind the meristem in the median plane of the thallus. The prothallus becomes symmetrically cordate, and has semicircular lateral wings (Fig. 28).

Occasionally, the establishment of an apical cell is much delayed. In such cases the first division of the terminal cell is by a vertical wall (parallel to the long axis of the filament instead of oblique) and soon a second wall is laid down at a right angle to the first. A broad spatulate prothallial plate is formed (Figs. 14–16) by divisions of the distal cells of the germ filament by walls

parallel to the long axis and by repeated longitudinal and transverse divisions in the daughter cells. This type of prothallial development is termed the *Drynaria*-type (Nayar and Kaur, 1969, 1971). The plate often becomes 5–10 cells wide and broadly ovate but is devoid of any organized meristem (Figs. 17, 21–24). An obconical meristematic cell is differentiated later by two oblique divisions in one of the marginal cells at the anterior end of the prothallial plate (Figs. 25, 26). Finally, a symmetrical cordate prothallus is formed.

In a few cases the terminal cell of the germ filament may not participate in the formation of the apical cell, or may be sluggish in doing so. In such cases, the obconical meristematic cell is formed behind the terminal cell by an oblique wall (Figs. 11, 12). Activity of this form of meristematic cell results in a spatulate prothallial plate. The meristematic activity may be restricted to one side of the plate, but ultimately an *Adiantum*-type, cordate prothallus is formed. Rarely, the germ filament is branched (Fig. 16), with each branch developing into separate gametophyte.

The mature prothallus is a typical heart-shaped structure with a prominent apical notch and takes about 128 days to develop from spore. The young gametophytes are entirely naked, being devoid of any hairs (Fig. 29). The rhizoids are hyaline. Until this stage of development, the midrib is undifferentiated and the sex-organs are not formed.

#### DISCUSSION

The early gametophyte development in Lomariopsidaceae has been classified primarily as *Drynaria*-type (Nayar and Kaur, 1971), or rarely the *Aspidium*-type as in *Elaphoglossum* (Stokey and Atkinson, 1957). The *Drynaria*-type of gametophyte development has been reported in a majority of the genera of Polypodiaceae (Nayar and Raza, 1970; Nayar and Kaur, 1971; Chandra, 1979; Chiou and Farrar, 1997; Perez-Garcia *et al.*, 2001). This type of development is also characteristic of some Athyrioideae, Cheiroleptaceae, Cyatheaceae, Dipteridaceae, Dryopteridaceae, Gleicheniaceae, Loxsomaceae, Thelypteridiaceae, (Nayar and Kaur, 1971).

The present study reveals that spore germination in *L. sorbifolia* is the typical *Vittaria*-type of polar germination, while prothallial development is primarily of the *Adiantum*-type as reported for the Dennstaedtiaceae (Nayar and Kaur, 1969). The *Adiantum*-type of prothallial development is characteristic of the families Dennstaedtiaceae, Grammitidaceae, Hypolepidaceae, Lindseaceae, Lygodiaceae and Plagiogyriaceae. In addition, it is also found in some genera of Cyatheaceae, Athyrioideae, Adiantaceae (*Adiantum*, *Coniogramme*) and occasionally of the families Dryopteridaceae (*Didymochlaena*), Aspleniaceae (some species of *Asplenium*), Blechnaceae (some species of *Blechnum*) and Cheilanthaceae (*Doryopteris*, some species of *Cheilanthus*) (Nayar and Kaur, 1969, 1971).

*Lomagramma sorbifolia* is unusual, so far as the development of the gametophyte (*Adiantum*-type) is concerned, relative to most of the other genera of the Lomariopsidoid ferns. However, it shows similarities with other

members of the Lomariopsidoid group, which have a *Drynaria*-type of development. The *Adiantum*-type of development has been considered to be more primitive than that of the *Drynaria*-type. In the *Adiantum*-type of development, growth and expansion of the prothallus is mainly through the activity of meristematic cells, whereas in the *Drynaria*-type of development the meristematic cells do not play a very active part in the growth and expansion of the young prothallus, as is the case for the majority of the Polypodiaceae (Nayar 1962, 1963, 1965).

Strap-shaped, lobed, or elongated prothallii (Atkinson, 1973), as reported in some of the Lomariopsidaceae (*Lomariopsis hederacea*, *Egenolfia vivipara*, *Bolbitis repanda* and *Elaphoglossum cuspidatum*), have not been observed in *L. sorbifolia*. The prothallus is naked throughout as reported for most species of *Bolbitis* and *Elaphoglossum*. The spores are bilateral and non-perinate as in *Thysanostoria* (Nayar and Kaur, 1965).

However, at least in some cases of *L. sorbifolia*, besides the *Drynaria*-type of early gametophyte development, the most common development is of *Adiantum*-type. Nayar and Kaur (1969) consider this an unusual feature among most of the other genera of the lomariopsidoid ferns. This supports the view of Holttum (1947), who considers them possibly to have been derived directly from a dennstaedtioid stock.

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